OBSERVATIONS ON THE LIFE HISTORY AND BIOLOGY OF AGROMYZA LATERELLA ZETTERSTEDT. (Diptera).*

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In the spring of 1916, while studying the interrelation of insects to certain swamp plants near Ithaca, New York, my attention was called to the occurrence of galls on the common wild blue flag, *Iris versicolor*. The plants then were from six to ten inches high, with three or four leaves out. The galls were always found on the outer leaf of the leaf-bundle, the

Figure 1

affected leaf ceasing to grow. This formation of the gall and the subsequent cessation of growth of the leaf very often affects the second or next inner leaf in a peculiar manner; the tip remains caught in the gall for some time, the growing leaf is bent out and in its rapid growth produces a number of wavy or undulating folds. Fig. 1 shows a photograph of a small group of plants with several galls and the characteristic appearance of the second leaf.

*Contribution from the Entomological Laboratory of Cornell University.

On cutting the gall open a small dipterous puparium was found inside. These puparia were taken to the laboratory, placed in vials, and on the 26th of May adult flies began to emerge. These were identified by Dr. O. A. Johannsen as *Agromyza laterella*.

In going over the literature on this species, I find that Thompson† reports having bred *A. laterella* (equals *magnicornis* Loew) from galls on blue flag. His paper is accompanied with an illustration of an iris leaf showing the gall. A short description of the gall is given. He suggests that the larval life seems to be completed the previous fall, but has not investigated this assumption.

With the adults emerging the latter part of May, the question naturally arose as to where the eggs would be placed, or in what stage the summer and fall would be spent, assuming that the winter was passed in the pupal stage. With this object in view a number of the adults were placed in cages with iris plants, in an effort to induce the flies to mate and oviposit; they failed, however, to reward the observer with either of these performances in captivity. It was found, though, that the adults were very common around iris plants, especially during the middle part of the day. At such times the females were carefully observed. They appear very nervous, darting here and there, and are easily disturbed. It was noticed that the females were stopping often to exert their ovipositors and work them on the tissue of the leaf. Such a leaf, later, showed a speckled appearance as shown in Plate II, Fig. 11. A number of these leaves were taken into the laboratory and an effort made to locate the eggs, but although these punctures or abrasions were very apparent, the eggs were not found.

It was while observing this "oviposition," that Dr. Needham suggested the possibility of having a case here, where the first generation of flies took on the leaf-mining habit, while the later, or second generation would be the ones producing the galls. Should this alternation of habits occur in the same species of insect, it would help to substantiate the theory that leaf-mining and gall-making are very closely related, the main

†Millet B. Thompson, Psyche Vol. XIV, 71–74, 1913. "Three galls made by Cyclorrhaphous Flies."

difference lying in the time of attack. The stimulus for the formation of the gall being given while the plant is young and the tissues are still forming; on the other hand, oviposition and the entrance of the larva into the leaf later, when the leaf has reached its main growth, does not stimulate the tissues to form any swelling whatsoever, the result being a mine.

Although no eggs were found, the plants were carefully watched for mines. On June 22, 1916, very delicate mines were found on the innermost leaves of the leaf-bundle. These mines are first noticeable on the outer surface, under the very thin epidermis of the leaf. The larvæ remain very close to the outer skin. The mines at first are so delicate as to be hardly perceptible to the naked eye, but with the aid of a magnifying glass, could be traced to the so-called egg-punctures, but no signs of the eggs were found.

In form the mine is linear, enlarging slightly as the larva proceeds downward and increases in size. The mine zigzags quite a little in its course, frequently the larva suddenly changes to the opposite side of the leaf, so that the mine is no longer visible on the upper surface, thus presenting a broken appearance. (Plate I, Fig. 1).

The color of the mine is white and shows plainly on the green leaf, but shows more plainly on the lower part of the leaf, which in the iris is of a purplish color.

The larva proceeds downward just about as rapidly as the new leaves are formed and come out of the leaf-bundle, and passes on, thus being in a situation where the tissue is newest and most tender. Sometimes, however, the larvæ may remain in the outer leaves and mine the entire length of it. This is especially true of the early larvæ. Plate I, Fig. 1 shows one of these outer leaves with the characteristic mines in it. It is not uncommon to find two or three larvæ working side by side in the same leaf, although each one maintains its own mine. The larvæ always maintain a lateral position in the mine, that is with the sides of the body toward the two surfaces of the leaf, always mining towards the base of the leaf; but just before pupation the larva assumes a position with the dorso-ventral sides towards the surfaces of the leaf, and with the anterior end upwards.

Puparia of these larvæ were first observed on July 25, 1916. In cases where larvæ reached maturity in the early or mid-summer, the puparia were always found at the base of one of the large outer leaves. Here the larva mines more to the center of the leaf-base, so that the mine is well within the tissue of the leaf and not visible from the outside. A somewhat enlarged excavation is made here, the larva assumes its position for pupation, and transformation occurs. The base of the leaf around the puparium swells just a little, thus showing a slight tendency toward gall-formation, (Plate II, Fig. 7).

Later in the fall the leaf is often found split open at the base, thus exposing the puparium. These puparia remain in this condition till the following spring.

Owing to the fact that oviposition stretches over a considerable length of time, (adults were seen around the iris plants for three or four weeks) different stages of larvæ were found in the iris all summer.

The larvæ in the fall of the year are always found mining on the innermost leaves of the leaf-bundle, and there in the very latest formed leaf, just as the plant ceases growth before the winter sets in, the larva enters and transforms into the puparium. Plate II, Fig. 9, shows the larva as it enters this inner leaf and Plate II, Fig. 10, shows the leaf after the larva has entered and pupated.

The iris plant does not die down completely in the fall, but the center remains alive, and usually on each side of the plant are formed offsets which produce the new plants the following spring. These offsets then may be regarded as new individuals, while the center represents the overwintering form of the old plant. Both center and offsets are protected from exposure by the old leaves which in the spring gradually drop to the ground and disintegrate. Plate II, Fig. 1 shows a plant with several offsets.

In the spring when the plant resumes its growth, it is the little leaf in the center which contains the puparium, that causes the characteristic gall. The second leaf, crumpled, stands there as an indicator, showing that the gall was formed while the second leaf was still rapidly growing.

All the various pupæ, those found early in the summer, as well as those found in the fall, and those in the galls, were, after emergence, identified as *A. laterella*.

These observations then proved that this was not a case of alternation of different habits in two generations, but it showed that the fly is an essential leaf-miner, that the entire larval stage is spent in leaf-mining; that the majority of the larvæ pupated at the base of the leaves where no typical galls were produced; that only those larvæ that developed slowly, and entered the innermost leaf late in the fall at the time of cessation of growth, were instrumental in bringing about the gall-formation. It would probably be a fair estimate to assume that not over 20–25% of the larvæ enter the inner leaf and form galls.

Just when or how the stimulus is brought about which causes the gall formation has not been determined. There is no sign of swelling in the fall, even after the pupa stage has been reached, but as soon as the plant resumes growth in the spring, the swelling occurs.

The galls and mines are common wherever the iris occurs, often nearly every plant is found to be affected. The fact that the gall is formed on the innermost leaf, explains the reason why only one gall occurs on the same plant. However on October 23, 1917, I found several instances where two larvæ were present in the same plant, both apparently descending down to the much coveted spot, the newly formed inner leaf. In each such instance I found that the second larva remained in the mine about 40–45 mm. above the other one which had entered the usual place, the innermost leaf of the bundle. The "upper" larva had excavated an enlarged place and transformed to the puparium. These puparia, found in this position above the other, are always more perfect in shape than those in the gall-forming leaf.

Description of Stages.

The Egg.

(Plate I, Fig. 3).

When dissected out of the ovary, the egg presents a glistening white appearance and measures from .36-.40 mm. in length, and .13-.15 mm. in width in its greatest thickness. The egg is elongate oval, tapering considerably towards one end, and more or less rounded at the other. The egg appears smooth, no markings are visible from the outside.

The Larva.

(Plate I, Fig. 2, and Plate II, Fig. 5).

The young living larva is almost pure white, later becoming a glistening creamy white. A light yellow line running longitudinally through the center of the body represents the alimentary canal. The innermost leaves of the leaf-bundle of the iris, not having been exposed to the sunlight, are of a light yellow color, and the presence of this color material in the alimentary canal is seen through the transparent skin of the larva.

The larva is long, cylindrical, measuring from 5–7 mm. in length, when full grown, and about 1.3–1.6 mm. in diameter. It tapers slightly toward either end. The head bears the black mandible or rasping organ with four teeth, the first two somewhat larger than the other two. (Plate II, Fig. 2). On the dorsal surface of the first thoracic segment, just back of the head, are found the two thoracic spiracles, borne on short brown stalks, flaring at each end with from 14–17 lobed projections on the outer margin. These lobes or tubercles have at the tip little openings which lead to the tracheal tube attached at the base. (Plate II, Fig. 3).

On the ventral surface of the three thoracic segments occur small transverse ambulatory ridges. The ridge on the first thoracic segment is considerably larger than the following ones.

On the last abdominal segment are found two brown anal spiracular projections, each of which ends in three down-curved lobes, at the tip of which are also found the small spiracles. (Plate II, Fig. 4).

Just before pupation the larva shortens and thickens considerably, the little ambulatory ridges are completely withdrawn, while the spiracular projections are fully extended, and the larval skin changes into the puparium.

The Pupa.

(Plate I, Fig. 8).

The pupæ vary considerably in form and size. A comparison of a number of pupæ showed that they varied in length from 3.10–4.66 mm., in width from 1.10–1.5 mm., and in thickness from 1.0–1.35 mm. Those that are found during the summer and early fall in the base of the leaf are more uniformly shaped being only slightly depressed; while those found later in the gall-forming leaf of the leaf bundle are always decidedly depressed and usually somewhat deformed, so that these pupæ in general appearance do not resemble the ones at the bases of the leaves and could be easily mistaken for another species.

The color of the puparium just after transformation is light brown, but later it becomes dark brown or almost black, especially those in the gall forming leaf; while the other puparia often remain rather light yellowish brown in color, though they also vary from dark brown to almost black.

During the transformation from the larval condition to the puparium, the thoracic and caudal spiracular projections are fully extended and transformed into two pairs of hardened hooks which help in holding the puparium in place in the plant.

The Adult.

(Plate I, Fig. 4).

The adults vary in length from 1.5–2.5 mm. The females are somewhat larger than the males. They are characterized by the proportionally large wings and the large antennæ, the antennæ of the males being larger than those of the females. The general ground color is shiny black or at least very dark brown. The thickened veins at the base of the wings, the halterers, proboscis, and joints of the legs are light yellow in color. Other lemon yellow markings occur along the sutures of the thorax and abdomen. The tibia and tarsi are yellowish brown. In the living flies the yellow markings are much more apparent than in the mounted dried specimens.

A technical description of the adult will be found in the Annals of the Entomological Society of America, VI, 300-301, 1913, by J. R. Malloch.

Specimens were found to be very numerous during the latter part of May till the middle or latter part of June, especially in the swamps and wet places where the iris grows in abundance.

EXPLANATION OF PLATES.

Plate I.

Fig. 1. Outer leaf of iris showing the characteristic mines made by the larva of *Agromyza laterella*. The broken places in the mines indicate where the larvae have mined to the opposite side of the leaf.
Fig. 2. Full grown larva, contracted, just before pupation.
Fig. 3. Egg, dissected out of the ovary of the female.
Fig. 4. Adult fly, female.
Fig. 5. A leaf-bundle cut open to show the course of the larva as it mines down towards the new forming leaf.
Fig. 6. Ovipositor of female, side view.
Fig. 7. Ovipositor of female, dorsal view.
Fig. 8. Pupa, dorsal view.
Fig. 9. A young iris plant in spring, showing the leaf-gall. Notice the evidence of the mine, indicated by the unshaded part in the tip of the leaf, where the larva entered the tip of the gall-forming leaf.

Plate II.

Fig. 1. *Iris versicolor*, showing the condition of the plant in late fall or winter. The unshaded leaves represent the old dried or dead leaves. The shaded leaves represent the green offsets which will form next year's growth. In the center of the old plant is found the pupa. This center also remains alive. The innermost leaf is represented by the dotted lines.
Fig. 2. Mandible or rasping organ of the larva of the iris fly.
Fig. 3. Thoracic spiracle of the larva.
Fig. 4. Anal spiracle of the larva.
Fig. 5. Nearly full grown larva.
Fig. 6. Cross section of a gall, showing the pupa in the center. Note the spongy nature of the gall.
Fig. 7. Basal portion of an outer leaf of iris, showing the little swelling produced by the early maturing larvae which pupate in this portion of the leaf.
Fig. 8. Cross section of an iris plant at *a* in Fig. 9. This shows the arrangement of the leaf-bundle. Each sheath has been separated slightly from the others to bring out the structure more plainly.
Fig. 9. Outer sheaths of the leaf-bundle torn away to show the larva entering the inner leaf just before pupation.
Fig. 10. Same as Fig. 9, after the larva has entered and pupated.
Fig. 11. Egg punctures on the leaf. The structure of the ovipositor indicates that these are abrasions, rather than punctures.

Note—Figures 2, 4, 8 and 9 of Plate I, and Figures 6 and 7 of Plate II, have been drawn for me by Miss Ellen Edmonson, of Lawrence, Kansas. The remaining figures are my own.